NECTAR SUGAR COMPOSITION IN SOME SPECIES OF AGAVE (AGAVACEAE)

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ABSTRACT

The nectar sugar composition of 19 species in the genus *Agave* was determined by high-performance liquid chromatography and found to be variable among species. Eleven species produced hexose-rich nectars with small amounts of sucrose, four species produced nectars that contained hexoses only, and four species produced sucrose-rich nectars. Known pollinators and visitors of four species are compared to expectations based on sugar composition.

The sugar composition of floral nectars is known to vary among species (Wykes 1952, Percival 1961), and coevolutionary relationships have been found between the proportions, or ratios, of different sugars and the kinds of pollinators attracted (Baker and Baker 1979, Spira 1981, Stiles 1976). However, it has also been suggested that some plant taxa are bound by "phylogenetic constraint" and do not develop the clear pollination syndromes seen in others (Baker and Baker 1979). Therefore, each study of plant-pollinator relationships will require knowing the overall capacity of the taxon under consideration to respond to evolutionary pressures. In addition, quantitative determinations of nectar sugars seem a prerequisite to more comprehensive and detailed theories of coevolution. The genus *Agave* has received recent attention as a model of plant-pollinator coevolution (Howell 1974; Schaffer and Schaffer 1977, 1979; Howell and Roth 1981), but few data are available on the nectar sugars within this genus. Our study examined the nectars of ecologically diverse species to determine if the nectar sugar composition varies among the taxa (perhaps reflecting different pollinators) or is relatively constant (perhaps indicating phylogenetic constraint).

MATERIALS AND METHODS

In most cases, flower clusters of appropriate age were collected in the field or botanical garden. They were washed carefully with a stream of deionized water, gently shaken dry, and left indoors overnight to

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produce nectar. The nectar was then removed with a micropipette and frozen until anlaysis. Samples from the Huntington Botanical Garden were collected, dried, and mailed to us in vials.

Sugars were identified and quantified by high-performance liquid chromatography (HPLC). A Waters Associates liquid chromatograph with a refractive index detector and Alltech Model 600NH column was used. The solvent was an acetonitrile : water (80:20 v/v) system at a flow rate of 2.0 ml/min. For calibration, regressions based on the response peak heights to standard sugar solutions were established. Quantities of each sugar in the nectar samples were determined by comparison to the calibrations and expressed as relative percent by weight. Injection volumes were 5–25 μl in 5 μl increments for calibrations and 10–25 μl in nectar samples.

Results and Discussion

Substantial differences exist in the proportions of sugars in the nectars of the taxa examined (Table 1). Eleven of the 19 species had nectars of the sFG type of Percival (1961), meaning that the nectars were rich in fructose and glucose with small amounts of sucrose. Four were of the FG type of Percival with only fructose and glucose. Two were the SFG type with nearly equal proportions of the sugars, and two were sucrose rich, the Sfg type. The first three types (FG, sFG and SFG) fall within the "sucrose poor" or "hexose rich" category of Baker and Baker (1979) because the ratio of sucrose to hexose is less than 0.5 in all of them. The Sfg nectars are in the "sucrose rich" category of Baker and Baker (1979) because this ratio is between 0.5 and 1.0. The agave samples have hexoses (fructose and glucose) in relative balance, with a tendency toward slightly higher concentrations of glucose. One species, *A. schottii* contained detectable quantities of maltose.

These data are also shown in Fig. 1, a ternary diagram well suited to illustrating systems with three components that sum to 100%. The data of Van Handel et al. (1972) for a broad spectrum of species from several families are shown for comparison. While none of the agaves we have examined so far is sucrose-dominated, the wide range of differences among the species supports the conclusion that the genus is without phylogenetic constraint.

The data suggest the probability of variation among pollinators or communities of pollinators, in habitats where agaves are found. Pollinator differences seem likely, because the species examined occur from sea level in arid and tropical Mexico to temperate grasslands and coniferous forests at elevations of up to 2200 m in the United States. That environment markedly affects the types of potential pollinators is well established (Arroyo et al. 1982, Primack 1978, Moldenke 1976, Pojar 1974, Cruden 1972, Downes 1965, Mani 1962).

TABLE 1. NECTAR SUGARS IN THE GENUS *Agave*. F indicates fructose, G glucose, S sucrose, M maltose, and R is the ratio of sucrose (plus maltose) to fructose plus glucose. HGB is the Huntington Botanical Garden, and DBG the Desert Botanical Garden. Locations in parentheses are the sources or type localities of garden plants. Replicates from the same locality were taken from different plants.

#	Species	Locality and elevation	% F	% G	% S	% M	R
Subgenus *Agave* (paniculate)							
1	*neomexicana*	Sacramento Mts., Otero Co., NM, 2250 m	46	54	0	0	0.0
2	*neomexicana*	Franklin Mts., El Paso Co., TX, 1200 m	40	60	0	0	0.0
3	*parryi*	Pinos Altos, Grant Co., NM, 2250 m	46	54	0	0	0.0
4	*shrevii*	HBG (type: Sierra Canelo, Chih., Méx.)	44	56	0	0	0.0
5	*fenzliana*	Revolcadero, Dgo., Méx., 1900 m	42	56	2	0	0.02
6	*chrysantha*	DBG (Pinal Co., AZ)	43	54	3	0	0.03
7	*chrysantha*	DBG (Pinal Co., AZ)	43	50	7	0	0.08
8	*zebra*	DBG (Sierra Viejo, Son., Méx., 700 m)	36	59	5	0	0.05
9	*mckelveyana*	DBG (Burro Ck., Yavapai Co., AZ, 700 m)	37	56	7	0	0.08
10	*palmeri*	Portal, Cochise Co., AZ, 1460 m	36	56	8	0	0.09
11	*palmeri*	Florida Mts., Luna Co., NM, 1580 m	52	36	12	0	0.14
12	*americana*	cult., El Paso Co., TX	39	49	12	0	0.14
13	*havardiana*	Chisos Mts., Brewster Co., TX, 1800 m	44	43	13	0	0.15
14	*pacifica*	Rio El Fuerte, Sin., Méx., 100 m	37	46	17	0	0.20
15	*colorata*	San Carlos, Son., Méx., 100 m	30	42	28	0	0.39
Subgenus *Litteae* (spicate)							
16	*utahensis*	Clark Mts., San Bernardino Co., CA, 1700 m	50	50	0	0	0.0
17	*pedunculifera*	El Palmito, Sin., Méx., 1875 m	40	51	9	0	0.10
18	*lechuguilla*	El Paso, El Paso Co., TX, 1120 m	40	50	10	0	0.11
19	*bracteosa*	HGB (type: Monterrey, N.L., Méx.)	47	21	32	0	0.47
20	*schottii*	22 km e. Douglas, Cochise Co., AZ, 1200 m	22	35	41	2	0.75
21	*toumeyana*	Sunflower, Maricopa Co., AZ, 1100 m	27	32	41	0	0.69
22	*toumeyana*	Sunflower, Maricopa Co., AZ, 1100 m	25	31	44	0	0.79

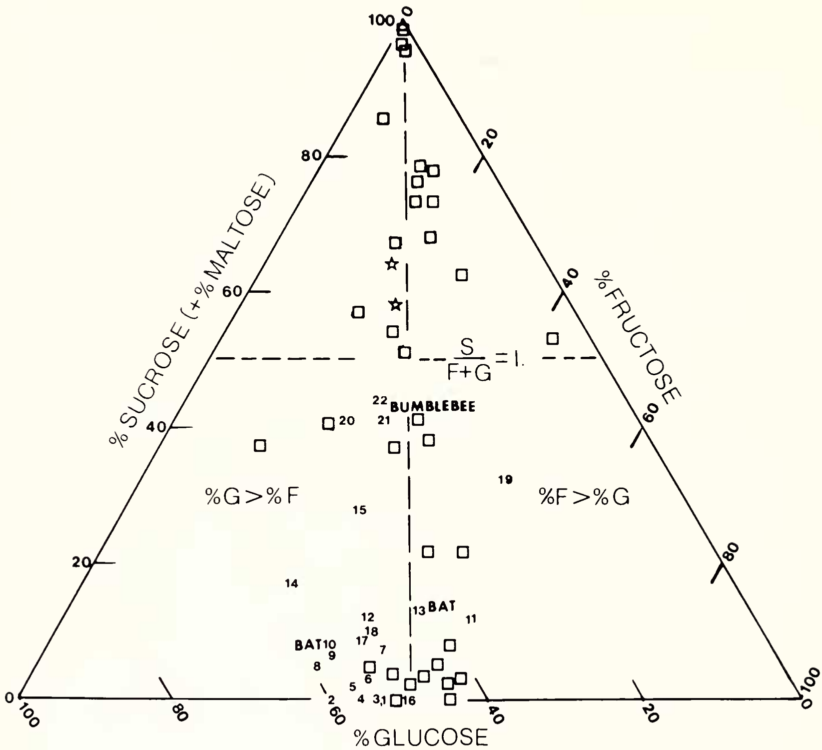

FIG. 1. Ternary diagram showing the distribution of sucrose (plus maltose), glucose, and fructose in floral nectars. Numerals indicate the *Agave* samples listed in Table 1, with two bat-pollinated taxa indicated. Open boxes are floral nectars from the survey of Van Handel et al. (1972), and the stars show two honeybee-pollinated plants (Bailey and Fieger 1954).

The pollination ecology of only two of the sucrose-poor species (*A. palmeri* and *A. havardiana*) is known in any detail. Baker and Baker (1979) suggest that the pollinators of species with sucrose-poor nectars are likely to be passerine birds, bats, flies, and some bees. Bats do exploit the nectar of *A. palmeri* (Howell and Roth 1981, Schaffer and Schaffer 1977) and *A. havardiana* (J. Kuban, pers. comm.). Other animals known to visit *A. havardiana* are passerine birds and hummingbirds (Allen and Neill 1979, Neill and Allen 1979), as well as many bees and other insects. Preliminary results of pollinator studies in *A. havardiana* indicate that bats and passerine birds are the most important pollinators, and that bees and hummingbirds are probably not of major significance (J. Kuban, pers. comm.). Although hummingbirds generally prefer sucrose-rich nectars, they also commonly utilize the nectars of sucrose-poor species in the mountains of Texas

(Allen and Neill 1979, Neill and Allen 1979), New Mexico (pers. obs.), and Durango (pers. obs.). Cruden (1972) notes that hummingbirds are much more common in the mountains of Mexico than at low elevations. In addition, Crosswhite and Crosswhite (1981) and Moldenke (1976) report that several species of hummingbirds visit *Agave* flowers. Perhaps the large quantity of nectar available is more important to hummingbirds than taste, as suggested by Stiles (1976).

Though most agaves have open flowers in which nectar is readily available to any visitor, *A. schottii* and *A. toumeyana* have tubular flowers. These species produce sucrose-rich nectars. Baker and Baker (1979) have stated that hummingbirds, hawkmoths, butterflies, and some bees prefer such nectars. Schaffer and Schaffer (1977) found that *A. schottii* and *A. toumeyana* were pollinated by carpenter bees (*Xylocopa*) and bumblebees (*Bombus*) and that bats are not important pollinators of *A. schottii* in southern Arizona. Schaffer and Schaffer (1977) pointed out that photographs of bats visiting these flowers (McGregor et al. 1962, Cockrum and Hayward 1962) were taken under artificial conditions using caged animals.

We found no evidence that nectar sugar composition is related to phylogeny, at least at the subgeneric level. Indeed, the subgenus *Litteae* contains nectars at the extremes of the genus (Table 1). It does seem that nectars of open-flowered species have very little or no sucrose, whereas higher sucrose levels are found near sea level and/or farther south. Further work is needed to determine whether this observation is real or an artifact of small numbers of species from lowland and or tropical areas.

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